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POLLEN MORPHOLOGY, CLASSIFICATION AND PHYLOGENY OF PALMAE

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Sommaire : Nous avons étudié les grains de pollen de 800 espèces appartenant à 193 des 226 genres des Palmiers. On y rencontre 27 types de pollen. L'endexine est pratiquement absente dans le pollen et il y a une sole épaisse. La Malaisie et la Nouvelle Guinée sont les centres de diversification maximum des Palmiers. Une classification nouvelle en tenant compte des corrélations entre les caractères morphologiques et polliniques a été établie. Nous avons retrouvé l'évolution des caractères polliniques et évalué la valeur phylogénique de neuf caractères morphologiques des Palmiers. Puisque chacune des sous-familles montre au moins quelques caractères évolués, aucune ne peut être considérée comme entièrement primitive. L'affinité palynologique des Palmiers est plus marquée avec les Liliales *s.l.* qu'avec les Arales.

Summary : There are 27 types of pollen grains in *Palmae*, 800 species belonging to 193 genera were studied. Endexine is practically absent. A thick foot layer is present. Malesia and New Guinea are the centres of maximum diversification of palms. A new classification based on the correlations between morphological and pollen characters has been proposed. We have traced the evolution of pollen characters and evaluated the phylogenetic value of nine morphological characters of palms. Since every one of the subfamilies show at least some evolved characters, none of them could be considered as entirely primitive. The palynological affinity of palms is more marked with the Liliales *s.l.* than with the Arales.

INTRODUCTION

Palms are the « Princes » of Plant Kingdom. This royal family has attracted the attention of several research workers. We have quite a lot of palm monographs. Yet our knowledge of this majestic family is far from complete. There are a number of classifications of palms but still there is a need of a better one. Whether the palms represent one family or an order of many families is a question raised often and again. The problem of their phylogenetic affinities is a much discussed one. We have therefore undertaken a thorough study of the pollen grains of this group and examined 800 species belonging to 193 of the 226 genera. We present here a brief resume of the most important results of our study. This constitute a part of the thesis[2] presented at the University of Montpellier (Thanikaimoni, 1970).

[1] This study has been completed in the Laboratoire de Palynologie, C.N.R.S., Montpellier (équipe de recherche n° 25) under the direction of Dr. M. Van Campo.

[2] Thèse inscrite aux archives originales du Centre de Documentation du C.N.R.S., 15, quai Anatole-France, Paris (VII^e) sous le numéro A.O. 4173.

TERMINOLOGY

APERTURE : sulcate = pollen with an elongated distal furrow.

Extensive-sulcate = pollen with the extremities of the sulcus extending beyond the equator.

Meridionosulcate = pollen with an annular furrow, distal in origin and encircling the pollen as a meridional girdle.

Ulcerate = pollen with a more or less circular distal aperture.

Colpate = pollen with elongated meridional furrow.

Porate = pollen with a more or less circular equatorial aperture.

EXINE : Ectexine consists of a thick foot layer (sole) on which we find the columella supporting a more or less perforated tectum. The exine of *Caryota* is intectate. In *Lepidocaryum*, the exine is spinulate with two sorts of spinules : small ones placed directly on the foot layer and big ones supported by columella.

Endexine is absent in the pollen grains of *Cocos nucifera*, *Caryota urens* and *Nypa fruticans* which we have studied with the help of electron microscope. This layer is absent or hardly visible in the pollen grains of the other species of palms observed with Wild M 20 microscope.

PRINCIPAL POLLEN TYPES AND THEIR GEOGRAPHICAL DISTRIBUTION

Based on the nature of aperture and ornamentation we recognize 27 pollen types. We give below their geographical distribution and the name of genera belonging to each type.

1. POLLEN MONOSULCATE; EXINE SMOOTH OR SCABROUS (TECTATE), FOVEOLATE OR FINELY RETICULATE (SEMITECTATE).

Pantropical : *Cocos.*

Africa, Madagascar, Asia : *Phœnix.*

Africa, Madagascar, Neotropics : *Raphia.*

Asia, Australia : *Actinokentia*, *Actinorhytis*, *Archontophœnix*, *Balaka*, *Basselinia*, *Bentinckia*, *Burretiokentia*, *Calyptrocalyx*, *Campecarpus*, *Clinostigma*, *Coleospadix*, *Corypha*, *Cyphokentia*, *Cyphophœnix*, *Cyphosperma*, *Cyrtostachys*, *Drymophlœus*, *Gigliolia*, *Gronophyllum gibbsianum*, *Gulubia*, *Heterospathe*, *Howeia*, *Hydriastele*, *Iguanura*, *Johannesteijsmannia*, *Kentiopsis*, *Laccospadix*, *Leopoldinia*, *Licuala*, *Linospadix*, *Livistona*, *Loxococcus*, *Nannorrhops*, *Neoveitchia*, *Normanbya*, *Orania*, *Paralinospadix*, *Pholidocarpus*, *Physokentia*, *Pigafetta*, *Pinanga rigida*, *P. Wrayi*, *Ptychandra clemensiana*, *P. glauca*, *Ptychococcus*, *Ptychoraphis*, *Ptychosperma*, *Rehderophœnix*, *Rhapidophyllum*, *Rhapis*, *Rhopalostylis*, *Satakentia*, *Solfia*, *Strongylocaryum*, *Trachycarpus*, *Veitchia.*

Africa : *Ancistrophyllum*, *Jubaeopsis*, *Oncocalamus*, *Podococcus.*

Madagascar region : *Acanthophœnix*, *Antongilia*, *Beccariophœnix*, *Chrysalidocarpus, Dictyosperma aureum, Dypsis heterophylla, Hyophorbe, Lodoicea, Marojejya, Mascarena, Neodypsis, Neophloga, Nephrosperma, Phloga schefferiana, Roscheria, Sindroa, Verschaffeltia, Vonitra.*

Neotropics : *Acœlorrhaphe, Acrocomia, Astrocaryum, Asterogyne, Bactris, Barbosa, Brahea, Butia, Calyptrogyne, Calyptronoma, Chamædorea, Chelyocarpus, Coccothrinax, Colpothrinax, Copernicia, Cryosophila, Erythea, Euterpe, Gastrococos, Gaussia, Geonoma, Hemithrinax, Hyospathe, Juania, Jubaea, Lytocaryum, Microcœlum, Morenia, Œnocarpus, Opsiandra, Parajubaea, Pholidostachys, Phytelephas, Polyandrococos, Prestœa, Reinhardtia, Rhyticocos, Sabal, Serenoa, Syagrus, Synechanthus, Tænianthera, Thrinax, Trithrinax, Washingtonia, Wendlandiella, Zombia.*

2. POLLEN MONOSULCATE, EXINE FOVEOLATE, FOSSULATE OR RUGULATE (SEMITECTATE).

Malesia : *Chambeyronia, Veitchia.*

Mascarenes : *Latania.*

Africa, Madagascar : *Elaeis s.s., Medemia.*

Neotropics : *Aiphanes, Allagoptera, Arecastrum Arikuryroba, Astrocaryum, Attalea, Bactris, Chamædorea, Coccothrinax, Corozo, Desmoncus, Geonoma spixiana, Jessenia, Manicaria, Markleya, Maximiliana, Metasocratea, Orbignya, Parascheelea, Rhopaloblaste, Roystonea, Scheelea, Syagrus coronata, Taenianthera acaulis, Thrinax radiata.*

3. POLLEN MONOSULCATE, EXINE COARSELY RETICULATE (SEMITECTATE).

Asia: *Adelonenga, Areca, Eugeissona brachystachys, Gronophyllum microcarpum, Gulubia macrospadix, Licuala peltata, L. spinosa, Nenga, Pinanga.*

Neotropics : *Acrocomia, Ceroxylon, Neonicholsonia, Pseudophœnix.*

4*a*. POLLEN MONOSULCATE, EXINE BACULATE (INTECTATE).

Asia, Australia : *Caryota* (operculate in *C. mitis, C. urens*).

Madagascar : *Dypsis, Phloga nodiflora.*

4*b*. POLLEN MONOSULCATE, EXINE CLAVATE AND BACULATE (INTECTATE).

Malesia : *Pinanga coronata* (clavæ supported by columella, free bacules in between columella).

5*a*. POLLEN MONOSULCATE, EXINE CLAVATE (INTECTATE).

Mauritius : *Deckenia.*

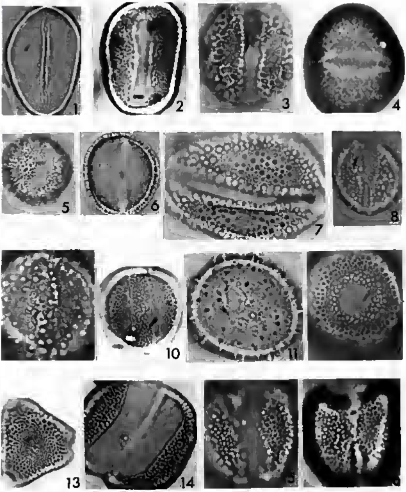
Neotropics : *Iriartea.*

5*b*. POLLEN MONOSULCATE, EXINE CLAVATE (TECTATE).

Malesia, Ceylon : *Oncosperma.*

6. POLLEN MONOSULCATE, EXINE GEMMULATE (INTECTATE?).

Indomalesia : *Pinanga hookeriana.*



Pl. 1. — **Calyptronoma dulcis** × 1 000; **2, Aiphanes caryotaefolia** × 1 000; **3, Nenga wendlandiana** var. **malaccensis** × 1 000; **4, Caryota urens** × 1 500, not acetolysed; **5, 6, Iriartea corneto** × 500; surface view and optical section; **7, Pinanga Hookeriana** × 1 000; **8, Cyrtostachys phanerolepis** × 500; **9, Catoblastus praemorsus** × 1 000; **10, Iriartella setigera** × 1 000; **11, Louvelia madagascariensis** × 1 000; **12, Louvelia albicans** × 1 000; **13, Sclerosperma Mannii** × 500; **14, Eugeissona tristis** × 100; **15, 16, Salacca edulis** × 1 000.

7. POLLEN MONOSULCATE, EXINE VERRUCATE (SEMITECTATE).
Malesia : *Cyrtostachys phanerolepis.*
Neotropics : *Bactris.*
Africa, Madagascar, Asia : *Borassus, Hyphæne.*

8*a*. POLLEN MONOSULCATE, EXINE SPINULATE (INTECTATE), SPINULES OF 2 TYPES : BIG AND SMALL.

Neotropics : *Catoblastus*, *Catostigma*, *Socratea*, *Wettinia*, *Wettiniicarpus*.
Asia, Australia : *Arenga*, *Caryota obtusa* var. *æquatorialis*, *Wallichia*.

8*b*. POLLEN MONOSULCATE, EXINE SPINULATE (INTECTATE?) SPINULES OF 2 TYPES : BIG ONES SUPPORTED BY COLUMELLA AND SMALL ONES NOT SUPPORTED BY COLUMELLA.
Neotropics : *Lepidocaryum*, *Mauritia*, *Mauritiella*.

8*c*. POLLEN MONOSULCATE, EXINE SPINULATE (SEMITECTATE).
S. E. Asia : *Pinanga Griffithii*.
Seychelles : *Phœnicophorium*.
Mauritius : *Dictyosperma album*.

9. POLLEN MONOSULCATE-PONTOPERCULATE, EXINE RETICULATE (SEMITECTATE).
Neotropics : *Iriartella*.
Mediterranean region : *Chamaerops*.

10. POLLEN ULCERATE, EXINE SPINULATE (TECTATE).
Madagascar : *Louvelia madagascariensis*, *Ravenea*.

11. POLLEN ULCERATE, EXINE RETICULATE (SEMITECTATE).
Madagascar : *Louvelia albicans*.
Malesia : *Areca catiso*, *Borassodendron*.
Neotropics : *Ammandra*.

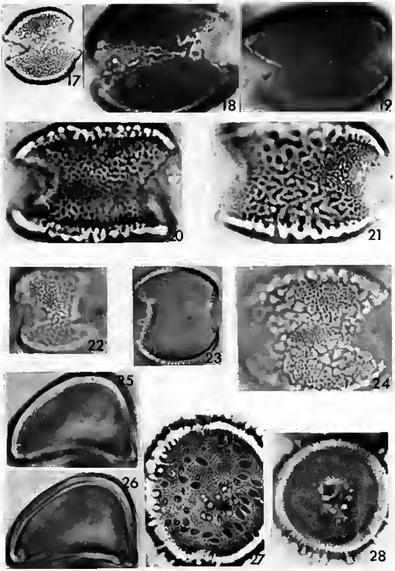
12. POLLEN TRIULCERATE, EXINE RETICULATE (SEMITECTATE).
West Africa : *Sclerosperma*.

13. POLLEN EXTENSIVE-SULCATE, EXINE FOVEOLATE OR FINELY RETICULATE (SEMITECTATE).
West Africa : *Eremospatha*.
S. E. Asia : *Plectocomia Griffithii*.

14. POLLEN EXTENSIVE-SULCATE, EXINE COARSELY RETICULATE (SEMITECTATE).
Malesia : *Eugeissona*.

15. POLLEN EXTENSIVE-SULCATE, EXINE CLAVATE (TECTATE).
Malesia, Ceylon : *Oncosperma*.

16. POLLEN EXTENSIVE-SULCATE, EXINE CLAVATE (INTECTATE); CLAVAE CROWNED WITH ONE TO FOUR SPINULES.
Malesia : *Korthalsia scaphigera*.



Pl. 2. — **17, Calamus andamanicus** × 500; **18, 19, Metroxylon sagu** × 1 000; distal and proximal views; **20, 21, Metroxylon salomonense** × 1 000; distal and proximal views; **22, 23, Daemonorhops fissa** × 1 000; surface view and optical section; **24, Calamus gracilis** × 1 000; **25, 26, Daemonorhops verticillaris** × 1 000; **27, 28, Korthalsia rigida** × 1 000; **27,** interporium; **28,** pore.

17. POLLEN MERIDIONOSULCATE, EXINE FINELY RETICULATE (SEMITECTATE).
S. E. Asia : *Plectocomia Griffithii.*

18*a*. POLLEN MERIDIONOSULCATE, EXINE CLAVATE (INTECTATE), CLAVAE CROWNED WITH ONE TO FOUR SPINULES.
Malesia : *Korthalsia laciniosa* (King's collector, 1884, CAL); *K. scaphigera.*

18*b*. POLLEN MERIDIONOSULCATE, EXINE CLAVATE (TECTATE).
Malesia : *Salacca edulis.*

19. POLLEN MERIDIONOSULCATE, EXINE SPINULATE (SEMITECTATE).
Asia, Australia : *Nypa*, *Salacca.*

20. POLLEN DICOLPATE, EXINE SMOOTH OR SCABROUS (TECTATE) OR FOVEOLATE OR FINELY RETICULATE (SEMITECTATE).
Africa, Asia : *Calamus.*
Asia : *Bejaudia*, *Ceratolobus*, *Daemonorhops*, *Metroxylon amicarum*, *M. sagu*, *Myrialepis*, *Plectocomia*, *Plectocomiopsis*, *Salacca secunda.*

21. POLLEN DICOLPATE, EXINE FOSSULATE AND RUGULATE (SEMITECTATE).
Asia : *Calamus.*

22. POLLEN DICOLPATE, EXINE COARSELY RETICULATE (SEMITECTATE).
Andaman Is., Salomon Is. : *Calamus longisetus*, *Metroxylon salomonense.*

23. POLLEN DICOLPATE, EXINE BACULATE (INTECTATE).
Andaman Is., Malesia : *Daemonorhops.*

24*a*. POLLEN DICOLPATE, EXINE CLAVATE (INTECTATE); CLAVAE CROWNED WITH ONE TO FOUR SPINULES.
Malesia : *Korthalsia tenuissima.*

24*b*. POLLEN DICOLPATE, EXINE SPINULATE (SEMITECTATE).
Malesia : *Ceratolobus glaucescens.*

25. POLLEN DICOLPATE, EXINE VERRUCATE (SEMITECTATE).
Asia, Australia : *Calamus*, *Cornera*, *Schizospatha.*

26. POLLEN DIPORATE, EXINE SMOOTH OR SCABROUS (TECTATE).
Malesia : *Eleiodoxa*, *Dæmonorhops verticillaris.*

27*a*. POLLEN DIPORATE, EXINE CLAVATE (INTECTATE); CLAVAE CROWNED WITH ONE TO FOUR SPINULES.
Malesia : *Korthalsia rigida* (rarely diporate-ulcerate).

27*b*. POLLEN DIPORATE, EXINE SPINULATE OR RARELY CLAVATE (INTECTATE); CLAVAE CROWNED WITH ONE TO FOUR SPINULES.
Malesia : *Korthalsia laciniosa* (Elmer, nº 16672).

It seems that Malesia and New Guinea are the centres of maximum diversification of palms. The neotropical region may be considered as another but less rich centre. The west african region is poor in genera and pollen types of palms. However, the triulcerate type is particular to this region. The Madagascar region, even though there is no *Coryphoideae* and very few *Lepidocaryoideae*, is rich in pollen types thanks to the *Arecoideae* which is well represented in this zone.

When we consider the distribution of the various pollen types in each of the nine subfamilies we note that the *Lepidocaryoideae* is the most diversified of all. We came across 17 pollen types in the 22 genera studied. Materials of the other three genera of this subfamily were not available for study. On the other hand, the *Arecoideæ* which contains as many as 124 genera, of which we have studied 105, has only 13 pollen types. Either the palynological diversification of this subfamily is very limited or many of the Arecoid genera do not merit the rank of a distinct genus. The situation is the same in *Cocoideae* with only 4 pollen types for 27 genera (total number of genera 28) and *Coryphoideae* with only 4 pollen types for 26 genera (total number of genera 34).

CLASSIFICATION OF PALMAE

We propose a provisional classification of palms taking into account the correlations between pollen characters and classical morphological characters.

I. — Fruit covered with scales; leaf pinnate (palmatifid or palmatinerved in Mauritieæ); vernation reduplicate; midrib with vascular bundles enclosed within a sclerotic cylinder; silica bodies of stegmata spherical; flower unisexual (bisexual in Korthalsieæ, Ancistrophylleæ, Eugeissoneæ); fruit simple; endocarp not perforated (except in Eugeissoneæ); seedling admotive. Pollen monosulcate in arborescent genera (except in *Metroxylon*), monosulcate or extensive-sulcate in genera with bisexual flower (except in *Korthalsia*); dicolpate, diporate, extensive-sulcate or meridionosulcate ...... *Lepidocaryoideae*.

II. — Fruit not covered with scales, leaf palmate, pinnate or bipinnate (simple in *Johannesteijsmannia*); vernation induplicate. Pollen never dicolpate or diporate :

1. Leaf palmate; midrib prominent with several independent vascular bundles; silica bodies of

stegmata spherical, simple fruit; seedling remotive :

a) Flower unisexual, endocarp perforated :
- — seed with a single or no furrow. Pollen monosulcate; exine foveolate, fossulate, areolate or verrucate..................... *Borassoideae.*
- — seed with many furrows. Pollen ulcerate; exine coarsely reticulate........ *Borassodendron.*

b) Flower bisexual or polygamous; endocarp not perforated.
- — Pollen monosulcate; exine smooth, scabrous, reticulate or foveolate .... *Coryphoideae.*
- — Pollen monosulcate-pontoperculate, exine reticulate .... *Chamaerops.*

2. Leaf pinnate with basal segments short and spinescents; midrib not prominent, little vasculated; silica bodies of stegmata spherical; endocarp not perforated; seedling remotive. Pollen monosulcate, exine reticulate .... *Phoenicoideae.*

3. Leaf pinnate or bipinnate, main ribs prominent, vascular bundles enclosed within a sclerotic cylinder; silica bodies of stegmata hat-shaped. Flower unisexual. Simple fruit; endocarp not perforated; seedling remotive. Pollen monosulcate: exine baculate or spinulate..... *Caryotoideae.*

III. — Fruit not covered with scales. Leaf pinnate; vernation reduplicate; midrib prominent, vascular bundles enclosed within a sclerotic cylinder. Flower unisexual except in *Pseudophoenix* with bisexual or polygamous flowers. Pollen never dicolpate or diporate :

1. Simple fruit; silica bodies of stegmata spherical or hat shaped; seedling remotive or admotive :

a) Endocarp perforated. Pollen monosulcate or brevisulcate; exine smooth, scabrous, foveolate, fossulate, reticulate or verrucate; never baculate, gemmulate, clavate or spinulate. *Cocoideae.*

b) Endocarp not perforated :
- — Pollen monosulcate, extensive-sulcate, ulcerate or brevisulcate; exine smooth, scabrous, finely or coarsely reticulate, fossulate, verrucate, gemmulate, clavate, baculate or spinulate .... *Arecoideae* (including *Manicaria*).
- — Pollen triulcerate, exine reticulate.... *Sclerosperma.*
- — Pollen monosulcate-pontoperculate, exine reticulate .... *Iriartella.*

2. Multiple fruit :

a) Ovary composed of 3 carpels, unilocular 1-3 ovuled, only one is fertile; silica bodies of stegmata hat-shaped; endocarp perforated; seedling viviparous. Pollen meridionosulcate, exine echinulate .... *Nypoideae.*

b) Ovary composed of 4-9 carpels, with equal number of 1-ovuled lobes all fertiles; silica bodies of stegmata spherical, endocarp not perforated; seedling remotive. Pollen monosulcate (*Phytelephas*) or ulcerate (*Ammandra*); exine reticulate .... *Phytelephantoideae.*

VALUE OF POLLEN CHARACTERS WITHIN THE SUBFAMILIES

ARECOIDEAE.

At the present state of our study we could not find any cogent correlation between the pollen characters and any other exomorphic characters of this subfamily.

BORASSOIDEAE.

We give below a classification of this subfamily emphasizing the correlation of classical characters and pollen characters.

I. — Seed with a single or no furrow. Pollen monosulcate :

- *a*) Stamens 6 in number; pollen verrucate :
  - — Homogenous endosperm. Pollen with distinct warts.
    - * Seed without furrow. Pollen size : L = 32-55 μ .... *Hyphœne.*
    - * Seed with furrow. Pollen size : L = 42-80 μ *Borassus.*
  - — Ruminate endosperm. Pollen with flat warts which are frequently fused into irregular areoles. Pollen size : L = 30-45 μ....... *Medemia.*
- *b*) Stamens numerous. Pollen with perforated tectum :
  - — Fruit very big. Male flowers numerous in the alveoles of the spadix. Pollen size : L = 75-90 μ; exine thickness 3 μ; perforations in the tectum 1 μ or less in diameter .... *Lodoicea.*
  - — Fruit small. Male flowers solitary in the alveoles of spadix. Pollen size : L = 52-72 μ; exine thickness 2.8-3.5 μ; perforations in the tectum irregularly distributed or fused into fossules *Latania.*

II. — Seed with many furrows. Pollen ulcerate, coarsely reticulate, pollen size : L = 90-100 μ............ *Borassodendron.*

CARYOTOIDEAE.

*** Leaf pinnate; endosperm homogenous; pollen monosulcate, spinulate.**

- **Pollen with spinules measuring 1.2-2.0 μ in diameter at the base and 2-3 μ in height .... *Arenga.***
- **Pollen with spinules measuring 1-1.5 μ in diameter at the base and 1.5-2 μ in height............ *Arenga porphyrocarpa.***
- **Pollen with spinules measuring 2-2.5 μ in diameter at the base and 4-5 μ in height.................. *Arenga pinnata.***
- **Pollen with spinules measuring 1 μ in diameter at the base and 1.5 μ in height .... *Wallichia.***

*** Leaf bipinnate; endosperm ruminate; pollen monosulcate, sometimes operculate; exine baculate.............. *Caryota.***

COCOIDEAE.

Cocos s. l.: All the variations of pollen morphological characters found among the species of *Cocos s. l.* (*Syagrus*, *Arecastrum*, *Rhyticocos*, *Barbosa*, *Arikuryroba*, *Microcoelum*, *Lytocaryum*, *Polyandrococos*, *Jubaea*, *Parajubaea*, *Jubaeopsis*, *Butia*, *Allagoptera*) overlap one another and sometimes they are seen in one and the same species (ex. *Cocos nucifera*). We therefore consider *Cocos* as a multispecific genus of wide distribution with its centre of gravity situated in tropical America.

Elaeis s. l. : Pollen morphological characters do not allow a separation of the three species of *Elæis* into three monotypic genera.

Attalea s. l. : When we examine the pollen grains of *Attalea s. l.* (*Maximiliana*, *Markleya*, *Orbignya*, *Scheelea*, *Parascheelea*) we note that there is a tendency towards the augmentation of the exine thickness and the reduction of aperture which finds its maximum expression in *Parascheelea*. Thus our study gives support to the contention that all these genera belong to but one large genus *Attalea* (PUNT and WESSELS BOER, 1966).

Bactris s. l. : The pollen grains of *Guilielma*, *Pyrenoglyphis*, and *Yuyuba* are not different from those of *Bactris*. Hence their inclusion in the latter is palynologically justified.

Acrocomia and *Gastrococos:* The only difference noticed between the pollen grains of these two genera lies in their size : *Acrocomia:* L = 62-70 μ; *Gastrococos:* L = 47-50 μ.

We have examined the pollen grains of only three species of *Acrocomia*. It is necessary to study the pollen grains of the remaining 22 genera of this genus to know whether small sized pollen grains are limited only to *Gastrococos*.

Astrocaryum: The two sub-genera of this genus are pollen morphologically very distinct :

Monogynanthus: aperture elongated, elliptical.

Pleiogynanthus: aperture wide, circular or triangular.

CORYPHOIDEAE.

On the whole the genera of this subfamily are very much similar in their pollen characters. There is no absolute correlation between pollen characters and other characters of this subfamily. We find all the three types of exine, simplibaculate, duplibaculate and pluribaculate, in one and the same pollen (ex. *Coccothrinax*, *Licuala*, *Sabal*, *Thrinax*, *Washingtonia*). It is equally difficult to separate the genera after the pollen size. The only genera which one could identify somewhat easily are *Cryosophila* with mostly trichotomosulcate pollen and *Chamaerops* with monosulcate-pontoperculate pollen.

LEPIDOCARYOIDEAE.

In the following classification we have tried to bring out the correlation of pollen characters with other characters.

I. — Leaf palmatifid or palmately nerved; arborescent palms; endocarp thin and membranous. Pollen monosulcate, sometimes brevisulcate or ulcerate .... *Mauritieae.*

II. — Leaf pinnate, very rarely digitate or penninerved :

  1. Arborescent palms :
    a) Bisexual palms; endocarp woody, porate at the base :
      Pollen monosulcate or extensive-sulcate.... ..... *Eugeissoneae* (only one genus, *Eugeissona*).
    b) Monoecious palms; endocarp thin, membranous:
      — seed ruminated. Pollen monosulcate, rarely ulcerate .... *Raphieae* (only one genus, *Raphia*).
      — seed not ruminated. Pollen dicolpate... .... *Metroxyleae* (only one genus, *Metroxylon*).
    c) Dioecious palms; endocarp thin and membranous. Pollen monosulcate..... *Salacceae : Pigafetta.*

  2. Cæspitose or stemless palms :
    a) Bisexual palms; endocarp woody, porate at the base.
      Pollen monosulcate or extensive-sulcate.... ..... *Eugeissoneae* (only one genus, *Eugeissona*).
    b) Dioecious palms. Endocarp thin and membranous.
      — seed not discoid. Pollen meridionosulcate (except in *Salacca secunda* with dicolpate pollen)..................... *Salacceae : Salacca.*
      — seed discoid. Pollen diporate. *Salacceae : Eleiodoxa.*

  3. Climbing palms or with lianous stem :
    a) Bisexual palms :
      * Rachis prolonged into a whip armed with

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* According to Wessels Boer (1965) *Mauritia*, *Mauritiella* and *Lepidocaryum* belong to one very natural and easily distinguishable genus. This opinion is corroborated also by our study : all the three are almost alike in pollen characters.

leaflets modified into hooks. Pollen monosulcate or extensive-sulcate...... *Ancistrophylleae.*
Spathe present. Pollen monosulcate.
Flowers in glomerules. Pollen with smooth to scabrous exine, size : L = 23-29 μ; exine thickness 1 μ............ *Oncocalamus.*
Flowers in pairs. Pollen with perforate tectum; perforations 1-2 μ. Pollen size : L = 42-68 μ exine thickness 3 μ *Ancistrophyllum.*
Spathe absent. Pollen extensive-sulcate.
Flowers in pairs. Pollen with foveolate exine; size : L = 42-55 μ........ *Eremospatha.*
* Adult leaf cirrhiferous, cirrhus armed with claws. Pollen meridionosulcate, extensive-sulcate or diporate; very rarely diporate-ulcerate.. *Korthalsieae* (only one genus, *Korthalsia*)
b) Dioecious palms. Pollen dicolpate; sometimes extensive-sulcate or meridionosulcate in *Plectocomia* ; rarely diporate in *Daemonorhops* .. *Calamaee.*

Note : We encounter a variety of pollen types within the genus *Calamus s. s.* The pollen characters of *Cornera*, *Schizospatha*, *Myrialepis*, *Plectocomiopsis* and *Ceratolobus* (with the exception of *C. glaucescens* having spinulate pollen) fall within the limit of pollen morphological variation of *Calamus s. s.* These genera are found to be similar also in anatomical characters (Tomlinson, 1961). The genus *Dæmonorhops* is morphologically and anatomically very distinct from *Calamus*. The species belonging to the section *Cymbospatha* of *Dæmonorhops* have a very particular type of exine : intectate-baculate. The pollen grains of the other section, *Piptospatha*, of this genus (with the exception of *D. verticillaris* having diporate pollen grains) are similar to those of *Calamus*.

NYPOIDEAE.

Nypa, the only genus of this subfamily, is pollen morphologically homogeneous.

PHOENICOIDEAE.

Phœnix, the only genus of this subfamily, is pollen morphologically homogeneous.

PHYTELEPHANTOIDEAE.

We recognize two genera within this subfamily : *Phytelephas* with monosulcate pollen and *Ammandra* with ulcerate pollen.

EVOLUTION OF POLLEN CHARACTERS

Evolution of aperture :

Before the appearance of Angiosperms, no pollen grains or spores were provided with exclusively equatorial functional aperture. How the equatorial aperture, an angiosperm feature is obtained? Is it accomplished by one, or more than one way? It seems that the *Palmæ* furnish us with good examples. In this family we encounter two evolutionary tendencies, one leading to dicolpate condition and the other resulting in meridionosulcate condition. Both of them are evolved from monosulcate condition through extensive-sulcate condition. In the first case, found in the subfamily *Lepidocaryoideæ*, the distal part of the extensive-sulcus is constricted and eliminated in order to give rise to two meridional colpus. In the second case, found in the subfamilies *Lepidocaryoideæ* and *Nypoideæ*, the two extremities of the extensive-sulcus fuse at the proximal pole to form a meridionosulcus that encircles the pollen like a meridional girdle. (The meridionosulcus should not be confused with the zonosulcus found in *Nymphæaceæ*. In the latter the aperture is more or less equatorial and not meridional in position.)

We have also observed two tendencies of reduction of aperture size : monosulcate to ulcerate (ex. *Mauritia*) and dicolpate to diporate (ex. *Dæmonorhops*).

The triulcerate pollen type of *Sclerosperma* seems to have resulted by the elimination of the central portion of trichotomosulcus.

The aperture of pollen grains of palms are generally covered with a smooth membrane. The operculate (*Caryota*), pontoperculate (*Chamærops*, *Iriartella*) and verrucate (*Metasocratea*) conditions appear to be secondary acquisitions of aperture membrane.

Evolution of exine :

It seems that there are two distinct tendencies of evolution of exine quite independent of aperture evolution. The pollen with tectate, smooth or scabrous exine possibly represents the basic type. The foveolate and reticulate types appear to be produced by the perforation of the tectum; a fusion of the perforations may lead to fossulate and areolate types.

The second tendency of exine evolution seem to be towards the development of various sculptural elements : the baculate type by a gradual dilation of the tip of the bacules could give rise to clavate type and a shortening of the pedunculate part of the clava could give rise to gemmulate type. In *Korthalsia* we have noticed a transition between clavate to spinulate type and in *Nypa* there is a transition from verrucate type to spinulate type.

The genera *Caryota* and *Wettinia* may be considered to exemplify a third tendency of exine evolution. In these genera there is no tectum. In *Lepidocaryum*, *Mauritia* and *Mauritiella* also a tectum is lacking, although the big spinules are supported by distinct columella.

DISCUSSION :

KUPRIANOVA (1948, 1954) and SOWUNMI (1967, 1968) have also considered the monosulcate type as primitive. But the former is of the opinion that the trichotomosulcus is more primitive than the atomosulcus while the latter derives the trichotomosulcus type from the atomosulcate type. In our opinion the trichotomosulcus, like the tetrachotomosulcus, is no more than a variation of the atomosulcus and it is not an index of evolution.

According to SOWUNMI the diporate condition is the result of suppression of the central part of the sulcus. In *Daemonorhops verticillaris* we have noticed no trace of sulcus at the distal part and the so-called disappearing colpus is but a fold in the proximal part of the pollen.

We have never observed a pollen with one distal furrow and one proximal furrow (type 7 in SOWUNMI, 1968) in *Palmæ*. Also, the tendency meridionosulcate to dicolpate does not exist in this family. The narrow gap between the distal extremities of the colpus and the large gap between the proximal extremities of the colpus suggest the derivation of dicolpate condition from extensive-sulcate type. Furthermore, in *Metroxylon* we have observed traces of disappearance of extensive-sulcus at the distal part of the pollen. We therefore consider that the dicolpate condition is derived from extensive-sulcate type and not by the mutilation of a meridionosulcus.

PHYLOGENETIC VALUE OF PRINCIPAL MORPHOLOGICAL CHARACTERS

Based on the results of our pollen study we have attempted to estimate the phylogenetic value of nine principal morphological characters of palms. We give below an outline of the evolutionary tendencies of these characters as perceived when we correlate them with pollen characters.

PERICARP : not scaly → scaly.

The scaly pericarp is considered as derived because the dicolpate and diporate pollen grains are found only in palms with scaly pericarp (*Lepidocaryoideae*).

FRUIT : simple → multiple.

The multiple fruit, formed out of several flowers having a common axis, is found in *Nypa* with meridionosulcate pollen. Hence we consider multiple fruit as an evolved character.

ENDOCARP : woody, perforated → membranous, not perforated.

In *Cocoideae* with primitive monosulcate pollen the endocarp is woody and perforated. In *Lepidocaryoideae* with derived pollen types the endocarp is membranous and not perforated.

The genus *Eugeissona* has Lepidocaryoid pericarp and Cocoid endocarp. Hence BECCARI (1918) has considered this genus as constituting a group intermediate to *Lepidocaryoideae* and *Cocoideae*. The presence of monosulcate and extensive-sulcate pollen types in *Eugeissona* seems to suggest that pollen morphologically also this genus occupies an intermediary position between these two subfamilies.

VERNATION : induplicate → reduplicate.

It is the reduplicate type of vernation that is observed in the evolved subfamilies as *Lepidocaryoideae* and *Nypoideae*. Hence we consider this character as evolved.

LEAF : palmate → pinnate → bipinnate.

According to ARBER (1922) the palmate leaf type is more primitive because it predominates among the fossil palms, whereas the pinnate leaf is the most common among the palms of the present day. EAMES (1953), on the other hand, is of the opinion that the palmate leaf is a telescoped form of pinnate leaf.

In the advanced families of *Nypoideae* and in the majority of *Lepidocaryoideae* we come across only pinnate leaf. Among the palm-leaved *Lepidocaryoideae* (*Maurilieae*) the palmate character is correlated with monosulcate pollen type. Hence we consider the palmate leaf type as primitive.

In *Phœnix* the basal leaflets are modified into spines. In *Ancistrophyllum* and *Desmoncus* the terminal leaflets are transformed into hooks. In *Caryota* the leaves are bipinnate. The leaves of these genera may be treated as representing derived types.

According to CORNER (1966) the bipinnate leaf of *Caryota* represents the ancestral form. This opinion is not acceptable because the bipinnate character is correlated with two other evolved characters : unisexual flower and intectate baculate pollen. The latter character is further correlated with scaly fruit in *Dæmonorhops* and reduced number of stamens in *Dypsis*.

FLOWER : bisexual → unisexual.

There are very few genera of palms with bisexual flowers. In all of them (except *Korthalsia*) we have monosulcate pollen. Hence we consider bisexuality as a primitive character. The genus *Korthalsia* needs further study. Whether its flowers like those of *Metroxylon*, another genus belonging to *Lepidocaryoideae*, are pseudohermaphrodite (physiologically unisexual) has to be verified.

Ovary : apocarpous → syncarpous (multicellular → unicellular).

Apocarpous ovary is found only in some *Coryphoideae* and it is correlated with primitive monosulcate pollen type.

Seedling : remotive → admotive → viviparous.

The seedling of *Coryphoideae* are remotive whereas those of *Lepidocaryoideae* are admotive. The latter type is therefore considered as evolved. The viviparous seedling of *Nypa* seems to be an adaptive modification of admotive type.

Stem : arborescent → acaulescent → rhizomatic.
↘ climbing.

According to Holttum (1955) solitary trunk may be derived from rhizomatic type with sympodial branching as a result of a suppression of the basal buds. But in the genera *Metroxylon* and *Nypa* with rhizomatic stem, we have advanced type of pollen grains. On the contrary, the arborescent genera of *Lepidocaryoideae* have primitive monosulcate pollen. We therefore conclude that arborescent habit is a primitive feature among palms. It is interesting to note that among the *Scitamineae* the tree habit is found to be primitive (Tomlinson, 1964).

All the climbing lepidocaryoid genera with axillary buds modified into cirrhiferous flagellum have evolved pollen types. Hence this habit seems to be an advanced character. The palms which climb by modified terminal leaflets appear to be less evolved because they (ex. *Ancistrophyllum*, *Desmoncus*) have primitive monosulcate pollen.

When we study a great number of palms, we are caught more by their resemblances than by their differences. It appears that they constitute a very natural family showing a number of overlapping tendencies. None of the nine subfamilies of *Palmae* can be considered as entirely primitive because every one of them has at least some evolved characters.

PALYNOLOGICAL AFFINITIES OF PALMAE

Corner (1966) holds the view that Monocotyledons are palm derivatives. There is no palynological evidence to support this view. On the other hand, we find in this family a number of pollen types and almost all of them are found in *Liliaceae*.

According to Rendle (1959) *Palmae* and *Araceae* are very closely related. But, we note that the inaperturate and periporate pollen types, as well as the pollen in tetrads, found in *Araceae* (Thanikaimoni, 1969) are absent in *Palmae*. While the Aroid pollen grains are, in majority of the cases, not resistent to acetolysis, the pollen grains of Palms withstand this treatment. Further, the striate exine type seen in some Aroids are unknown in *Palmae*. Thus the palynological affinities of *Palmae* are more with *Liliaceae* than with *Araceae*.

In Corner's opinion, *Cyclanthaceae* could have evolved from the ancestry of *Phytelephas* because both *Cyclanthaceae* and *Phytelephas* are limited to tropical America. We note that *Palmae* and *Cyclanthaceae* have in common the following evolutionary tendency : monosulcate → ulcerate. But the dicolpate and meridionosulcate pollen types found in *Palmæ* are unknown in *Cyclanthaceae*. The derivation of diporate pollen type by the elimination of the central position of the sulcus, observed in *Cyclanthaceae* (Harling, 1958) is yet to be demonstrated in *Palmae*.

Pollen grains comparable to those of *Mauritia* are observed in *Pandanaceae*. But in this family we do not have the meridionosulcate pollen type of *Nypa*, a genus to which it is said to have close affinity (Corner, 1966).

The Agavales, according to Hutchinson (1959), represent a link between Palmales and Liliales. The occurrence of dicolpate pollen grains in these groups may be considered as a sign of affinity.

Good (1956) considers the palms are distinct biological group. He has provided a stellar model of Monocotyledons in which the palms occupy a peripheral position. But pollen morphologically the palms fall within the sphere of affinities of his « hard core » of Monocotyledons.

Our study has enabled us to confirm that « l'avantage des grains de pollen pour traiter un sujet aussi vaste et important que la classification est de pouvoir embrasser d'un seul coup d'œil des centaines d'individus et d'un seul coup d'œil des dizaines de caractères et d'avoir de façon presque immédiate une idée des variations maximales d'un ensemble » (Van Campo, 1967). We have used pollen characters as a tool to test affinities between genera and families and emphasized them in our tentative classification of palms.

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